

AGE-SPECIFIC STOPOVER BEHAVIOR OF MIGRANT BALD EAGLES

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ABSTRACT.—A review of stopover behavior in birds revealed that most migrate as quickly as fuel reserves allowed (i.e., were time minimizers). This pattern stemmed from studies conducted almost exclusively on small-bodied species (< 50 g), which migrate primarily by flapping flight. However, body size has a significant effect on metabolic rate and costs of locomotion, two characteristics with direct relevance to migration and stopover behavior. I examined the autumn stopover behavior of a large-bodied species (4–5.5 kg) that migrates by soaring. I captured and radio-tagged 68 Bald Eagles (*Haliaeetus leucocephalus*) at Hauser Reservoir, Montana from 1992–1994. After capture, juveniles stayed at the stopover site longer than older eagles. Body condition was similar between the two age groups and did not correlate with post capture residence time. Consumption rates of eagles were not age-specific. Juvenile and 1.5-year old eagles had similar consumption rates and body condition, but differed in residence times, which suggested that experience modified stopover behavior. Stopover behavior of Bald Eagles supported the hypothesis that large species are less sensitive than small species to body condition and consumption rates during migration. Received 29 April 1999, accepted 24 August 1999.

During the journey between breeding and wintering grounds, migrating birds must make many important decisions: when to migrate, what route to take, and where to rest and feed (Gwinner 1977, Kerlinger 1989, Berthold and Terrill 1991). The behavior of birds at migratory stopovers, those places used for resting and replenishing depleted energy reserves, is of particular ecological interest because it is there that migrants must balance time and energy constraints, reconcile conflicting demands of foraging and predator avoidance, and evaluate weather conditions. Researchers find it difficult to determine how these factors affect stopover behavior because they often interact. Investigation of this problem is further complicated because strategies differ between spring and autumn migration (O'Reilly and Wingfield 1995, Yong et al. 1998).

Theoretical models of stopover duration provide quantitative and qualitative predictions that discriminate among species that attempt to maximize energy gain, minimize time enroute, or minimize energy expended during migration (Stephens and Krebs 1986, Alerstam and Lindström 1990). A review of field studies reveals that predictions of the time-minimization hypothesis accord with the

stopover behavior of most small passerines and waders (Alerstam and Lindström 1990). Individuals in better condition (i.e., higher fat load) or that deposited fat quickly (i.e., higher consumption rate) had short stopovers.

Information regarding the stopover behavior of large-bodied migrants, species orders of magnitude larger than passerines and waders, is lacking. These data are potentially important because large birds have lower mass-specific metabolic rates than passerines and exhibit energy saving soaring flight (Kerlinger 1989, Hedenström 1993), two characteristics with direct relevance to models addressing migration behavior. Large birds should be less sensitive than small birds to the effects of body condition and consumption rates when deciding how long to remain at migratory stopovers.

I studied the stopover behavior of Bald Eagles (*Haliaeetus leucocephalus*), a large-bodied species (4–5.5 kg) that must stop to rest and feed during its 2000 km autumn migration across western North America (McClelland et al. 1994). First, I tested hypotheses that stopover duration of eagles is related to body condition and consumption rate. Second, I examined age-specific differences in stopover lengths. In previous studies, adult birds usually had shorter stopovers than juveniles, which tended to be in poor condition and needed additional time to replenish fat reserves before continuing migration (Serie and Sharp 1989; Ellegren 1991; Carpenter et al.

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1993a, b; Holmgren et al. 1993, Yong et al. 1998). Therefore, I predicted that if differences in stopover length existed between older and younger eagles, they would be due to differences in body condition or consumption rate. Age groups in better condition or which have higher consumption rates should have shorter stopovers.

METHODS

This study was conducted at Hauser Reservoir, a 23 km long impoundment of the upper Missouri River in west-central Montana (46° 41' N, 111° 49' W). Before 1989, Bald Eagles migrated quickly through the area during autumn, but after an introduced kokanee salmon (*Oncorhynchus nerka*) population proliferated. During the 1980s, hundreds of eagles began to congregate from October to December to feed on spawning and dead salmon. Over 7500 people visited the site annually to view eagles. The first 7 km of river below the dam and adjacent public shoreline was closed from mid-October to mid-December to protect eagles from human disturbance.

At least twice a week from mid-October to late November 1992–1994, several assistants and I captured eagles with padded, No. 3N double-spring leg-hold traps set around salmon carcass baits staked in shallow shoreline water (see Harmata 1985, McClelland et al. 1994 for detailed methodology). We watched trapping sites continuously from a distance of less than 1.6 km and removed eagles from traps within 5 min of capture.

Bald Eagles were banded, measured (Bortolotti 1984, Garcelon et al. 1985, McClelland et al. 1998), and aged (McCullough 1989). I did not rank body condition using the traditional index of mass/wing chord because wing chord differed among eagle age classes (Bortolotti 1984, McClelland et al. 1998), and most eagles captured during autumn at Hauser Reservoir had broken or heavily worn primary feathers. Instead, I ranked body condition using two other indices: (1) mass (g)/bill depth (mm) and (2) mass (g)/tarsal width (mm), measured anteriorly/posteriorly (AP; see Garcelon et al. 1985, McClelland et al. 1998). Because estimating body condition of migrants was species-specific (Spengler et al. 1995, Winker 1995), I used bill depth and tarsal width to correct for body mass because these two measurements best reflected size in Bald Eagles (see Bortolotti 1984, Garcelon et al. 1985). The relationship between bill measurements (culmen, bill depth) and body mass has also been used to rank body condition of soaring hawks (Gorney and Yom-Tov 1994). Bald Eagles of different ages that migrated through Montana had similar masses, bill depths, and tarsal widths (McClelland et al. 1998), so age-specific size did not confound interpretation of either condition index.

I used radio telemetry to estimate residence times because recapture and resighting data assume equal error among age or body condition groups. I fitted the

first 20–25 eagles captured each season with radio transmitters (25 g; L. L. Electronics, Mahomet, Illinois) mounted ventrally to the two center retrices (Kenward 1978). It took 30–45 min to process each eagle and all were released within sight (< 1 km) of the trapping area. I used a hand-held, three-element yagi antenna to determine the presence or absence and location of radio-tagged eagles at least once a day during both daylight and evening hours (in roosts). Post capture residence time was calculated for each radio-tagged eagle by subtracting the date of capture from the date the eagle was last detected at Hauser Reservoir plus one day (Biebach et al. 1986).

Two observers recorded the foraging behavior of Bald Eagles from a vehicle parked 20–150 m from the primary salmon spawning and eagle foraging sites located along approximately 500 m of river. Observers used spotting scopes (20–60×) and binoculars (10×) to watch foraging eagles. Observations were made at least three times per week from late October to mid-December 1992–1994 in each of two time periods: 0.5 h before sunrise to noon and noon to 0.5 h after sunset. Foraging eagles were aged (juvenile; 1.5, 2.5, 3.5 year old; adult) using plumage, cere, and eye coloration (McCullough 1989). Observers attempted to record every foraging attempt, and recorded the time and estimated the fraction of salmon consumed (0, 1/3, 2/3, whole). Observations of individual foraging bouts began when eagles secured a salmon and ended when the salmon was consumed, dropped, or lost to a pirating conspecific.

In 1994 I collected 11 spawning salmon with a dip net and 11 salmon carcasses along the shoreline to determine caloric content. Each salmon was weighed in the field (wet, nearest 25 g) and frozen. In the laboratory, salmon were thawed, dried to constant weight (nearest g) in a convection oven (50–60°C), and ground into a homogenate using a Waring blender. Caloric content of duplicate samples from each salmon was determined using a semi-micro bomb calorimeter (Parr, model 1411). Forty salmon carcasses (20 of each sex) were also weighed (nearest 25 g) each autumn to obtain mean annual mass. Mean mass of live salmon (1992–1994) was obtained from state fisheries biologists.

Mass of salmon carcasses was similar among years (ANOVA: $F = 0.50$, $df = 2, 117$, $P > 0.05$). I used mean mass of live (1992: 1055 g, $n = 203$; 1993: 1101, $n = 63$; 1994: 1073 g, $n = 85$) or dead (1992: 831 g, $n = 40$; 1993: 883 g, $n = 40$; 1994: 860 g, $n = 40$) salmon multiplied by mean caloric content (live: 0.86 kcal/g, $n = 11$; carcass: 0.71 kcal/g, $n = 11$) and the fraction of salmon consumed to determine energy gain for each foraging attempt. I estimated consumption rates of Bald Eagles feeding at Hauser Reservoir on a sample of 3182 foraging attempts over 38 days of observation. Following the methods of Stalmaster and Gessaman (1984), I estimated mean daily energy intake for each eagle age class by dividing the total daily energy intake of each age class by the maximum

daily count of similarly aged eagles recorded at one hour intervals during foraging observations.

Once a week from late September through December 1992–1994, a four person team conducted surveys by motorboat to estimate the number of eagles congregating at Hauser Reservoir. Surveys began between 09:00 and 10:00 MST. The boat travelled at 5–10 kph and at least three observers independently counted eagles. Counts were averaged to produce the survey total. I also determined relative prey abundance by counting the number of salmon carcasses on and within 2 m of two shoreline transects (1.6 km total) in the primary spawning reach. Using a headlamp, I counted carcasses 1.5 h before sunrise the day of eagle surveys.

When necessary, I transformed (log and square root) data (residence times, condition indices, consumption rates) prior to analyses (SPSS, Inc. 1998, version 8.0) to achieve normal distributions (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). I have reported untransformed means (± 1 SE) in text, tables, and the figure to facilitate interpretation. I used ANOVA and *t*-tests to compare means (condition indices, consumption rates, capture dates) among or between age groups (all age classes or juveniles vs older eagles), respectively. Simple linear regression was used to detect relationships between post capture residence time and (1) body condition, (2) date of capture, and (3) time of capture. Simple linear regression was also used to examine the relationship between weekly counts of eagles and salmon. I used χ^2 tests to analyze two departure conditions: eagles leaving day of capture versus other eagles by age class and by crop condition.

RESULTS

Each year migrant Bald Eagles began to congregate at Hauser Reservoir in early October; weekly counts of both eagles and kokanee salmon peaked in mid-November. Each year the number of eagles and salmon were highly correlated (Fig. 1). Despite the ten-fold fluctuation in peak number of salmon carcasses among years, peak number of eagles was similar from 1992–1994.

We captured 99 eagles at Hauser Reservoir from 1992–1994. Not one eagle was recaptured within or across years. Most (86%) of the eagles we radio-tagged ($n = 68$) were captured before peak salmon counts, and overall residence time following capture averaged 10.4 (1.4) days. Radio-tagged eagles departed the stopover site continuously throughout each autumn. In 1992 marked eagles ($n = 23$) left on 17 different dates; in 1993 marked eagles ($n = 20$) left on 16 different dates; and in 1994 marked eagles ($n = 25$) left on 17 different dates. Few (9%) radio-tagged eagles, all of which were juveniles, remained at Hau-

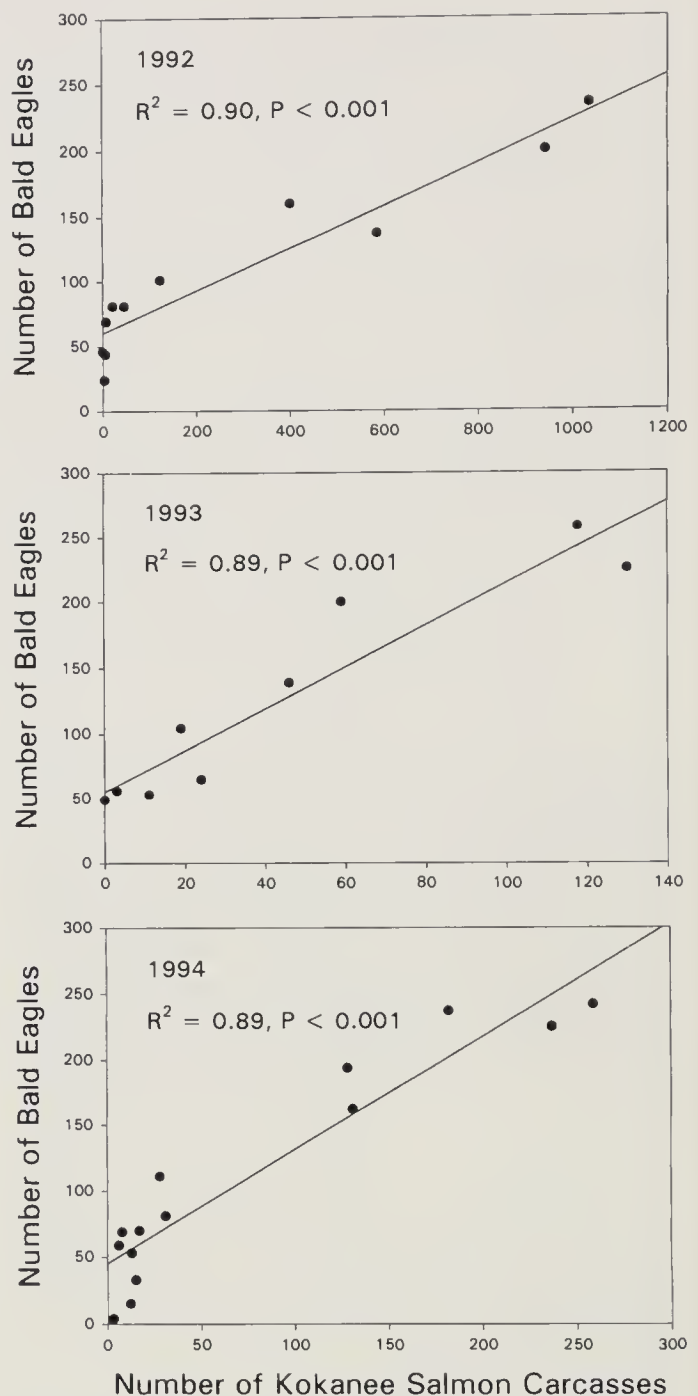


FIG. 1. Relationship between weekly number of Bald Eagles and kokanee salmon carcasses at Hauser Reservoir, Montana. Note that scales on x-axes differ.

ser Reservoir into December. Latest departure dates of radio-tagged eagles were 14 December 1992, 25 November 1993, and 9 December 1994. Most (> 90%) of the reservoir had frozen by mid- to late December and fewer than 15 eagles remained in the area during winter.

Post capture residence times of radio-tagged eagles were similar among years (Table 1), so yearly data were combined for other analyses. After capture, juveniles remained at Hauser Reservoir significantly longer than

TABLE 1. Post capture residence times and consumption rates of Bald Eagles radio-tagged at Hauser Reservoir, Montana. Age classes: juvenile (JUV); 1.5, 2.5, 3.5 year old; adult (AD). Sample size for consumption rates is number of days foraging was observed.

| | Residence time (days) | | Daily consumption rate (kcal/eagle) | |
|-------------------|-----------------------|----------|-------------------------------------|----------|
| | \bar{x} (SE) | <i>n</i> | \bar{x} (SE) | <i>n</i> |
| Year ^a | | | | |
| 1992 | 9.7 (2.4) | 23 | 536 (33) | 14 |
| 1993 | 13.9 (2.6) | 20 | 540 (42) | 13 |
| 1994 | 8.4 (2.3) | 25 | 552 (24) | 11 |
| Age ^b | | | | |
| JUV | 14.5 (1.9) | 41 | 457 (36) | 38 |
| 1.5 | 4.7 (2.1) | 14 | 453 (36) | 37 |
| 2.5 | 4.2 (2.6) | 6 | 576 (52) | 37 |
| 3.5 | 4.0 (1.3) | 5 | 452 (63) | 31 |
| AD | 1.5 (0.5) | 2 | 703 (42) | 38 |
| Sex ^c | | | | |
| Male | 10.0 (1.7) | 45 | | |
| Female | 11.3 (2.5) | 23 | | |

^a Residence time: $F = 2.11$, $df = 2, 65$, $P > 0.05$; Consumption rates: $F = 0.04$, $df = 2, 35$, $P > 0.05$.

^b Residence time: juveniles versus older eagles: $t = 4.58$, $df = 66$, $P < 0.001$; Consumption rates: $F = 6.02$, $df = 4$ and 176 , $P < 0.001$ (AD > JUV, 1.5 and 3.5 year olds).

^c $t = 0.44$, $df = 66$, $P > 0.05$.

older eagles (Table 1). The four older age classes had similar residence times following capture and were combined to increase statistical power. Older eagles left Hauser Reservoir the day of capture more often than juveniles ($\chi^2 = 7.41$, $df = 1$, $P = 0.007$), although no trend existed within the older age group: 1.5 year old (36% left day of capture), 2.5 year old (67%), 3.5 year old (0%), and adult (50%). I excluded eagles that left the day of capture to reduce the potential effect of age-specific handling stress and reanalyzed the comparison between age groups. Older eagles still had shorter residence times following capture than juveniles ($t = 3.07$, $df = 52$, $P = 0.003$). Residence times were similar for male and female eagles ($t = 0.44$, $df = 66$, $P > 0.05$; Table 1).

The body condition indices of radio-tagged juvenile eagles were similar to those of radio-tagged older eagles (Table 2). No relationship existed between post capture residence time and either condition index for the entire eagle sample (mass/bill depth: $R^2 = 0.01$, $P > 0.05$, $n = 48$; mass/tarsus AP: $R^2 = 0.06$, $P > 0.05$, $n = 46$) or for each age group (mass/bill

TABLE 2. Body condition indices of Bald Eagles congregating at Hauser Reservoir, Montana. Age classes: juvenile (JUV); 1.5, 2.5, 3.5 year old; adult (AD).

| | Mass (g)/Bill depth (mm) ^a | | Mass (g)/Tarsus AP (mm) ^b | |
|-----|---------------------------------------|----------|--------------------------------------|----------|
| | \bar{x} (SE) | <i>n</i> | \bar{x} (SE) | <i>n</i> |
| Juv | 138.0 (3.5) | 21 | 281.9 (6.0) | 19 |
| 1.5 | 136.7 (3.4) | 14 | 278.0 (6.2) | 14 |
| 2.5 | 141.1 (4.4) | 6 | 276.0 (10.4) | 6 |
| 3.5 | 132.7 (6.9) | 5 | 263.7 (9.7) | 5 |
| AD | 120.3 (5.2) | 2 | 243.5 (1.8) | 2 |

^a Juveniles versus older eagles: $t = 0.55$, $df = 46$, $P > 0.05$.

^b Juveniles versus older eagles: $t = 1.22$, $df = 44$, $P > 0.05$.

depth: juveniles: $R^2 = 0.01$, $P > 0.05$, $n = 21$; older eagles: $R^2 = 0.10$, $P > 0.05$, $n = 27$; mass/tarsus AP: juveniles: $R^2 = 0.03$, $P > 0.05$, $n = 19$; older eagles: $R^2 = 0.09$, $P > 0.05$, $n = 27$). However, some eagles were captured with full crops (> 500 g), which may have added a large amount of variation to the condition estimates. To eliminate this potential bias, I repeated regressions using only eagles captured with empty crops. A significant relationship between post capture residence time and body condition (mass/tarsus AP) was evident, but the amount of variation explained was low (mass/bill depth: $R^2 = 0.01$, $P > 0.05$, $n = 32$; mass/tarsus AP: $R^2 = 0.14$, $P = 0.021$, $n = 31$). More importantly, the trend was opposite that expected: eagles in good condition stayed longer after capture than those in poor condition. Eagles captured with full, half full, or empty crops were equally likely to depart Hauser Reservoir the day of capture (juveniles: $\chi^2 = 4.53$, $df = 2$, $P > 0.05$; older eagles: $\chi^2 = 3.95$, $df = 2$, $P > 0.05$).

Although we captured juvenile eagles earlier during the season than older eagles ($t = 2.51$, $df = 66$, $P = 0.014$), date of capture explained little variation in post capture residence time for all eagles combined ($R^2 = 0.10$, $P = 0.005$, $n = 68$), or for each age group (juveniles: $R^2 = 0.01$, $P > 0.05$, $n = 41$; older eagles: $R^2 = 0.09$, $P > 0.05$, $n = 27$). The time of day of capture, a possible indicator of early morning foraging and recent mass gain that can affect estimates of condition (see Winker et al. 1992), was unrelated to post capture residence time for all eagles ($R^2 = 0.00$, $P > 0.05$, $n = 68$), or for each age group (juveniles: $R^2 = 0.00$, $P > 0.05$, n

TABLE 3. Mean (SE) consumption rates (kcal/eagle/day) of Bald Eagles feeding on kokanee salmon at Hauser Reservoir, Montana. Values were calculated for each week and dates shown correspond to mid-week. Sample size is number of days foraging was observed.

| Year | Date ^a | | | | | n |
|------|-------------------|----------|-----------|-----------|-----------|----|
| | 11/1 | 11/8 | 11/15 | 11/22 | 11/29 | |
| 1992 | 419 (16) | 601 (71) | 526 (74) | 560 (69) | 504 (128) | 14 |
| 1993 | 483 (190) | 573 (75) | 609 (51) | 427 (102) | 617 (96) | 13 |
| 1994 | 509 (12) | 552 (64) | 806 (190) | 510 (121) | 387 (113) | 11 |

^a $F = 186, 4, 32$ df, $P > 0.05$.

= 41; older eagles: $R^2 = 0.07, P > 0.05, n = 27$).

Mean daily consumption rates of eagles feeding on salmon did not differ among years (Table 1) or among days within years (Table 3). All yearly data were combined to estimate mean daily consumption rates for each eagle age class. High density and frequent movement of eagles at Hauser Reservoir made it difficult to locate and record foraging behavior of radio-tagged individuals. Therefore, I followed the methods of Loria and Moore (1990) and calculated consumption rates of similarly aged eagles and used those values as intake estimates for each age class of radio-tagged eagles. Adult eagles had higher mean daily consumption rates ($F = 6.02, df = 4, 176, P < 0.001$) than juveniles, 1.5 year old, and 3.5 year old eagles (Table 1).

DISCUSSION

Body condition of Bald Eagles at capture does not predict post capture residence time during autumn migration. In contrast, body condition of migrating ducks, shorebirds, and passerines correlates with duration of autumn stopovers (Cherry 1982, Biebach et al. 1986, Dunn et al. 1988, Serie and Sharp 1989, Ellegren 1991). These species usually gain a large percentage (40–60%) of normal body mass at stopovers to offset energetic costs associated with heavy wing-loading, migration using energetically expensive flapping flight, and long range movements. However, eagles have low mass-specific metabolic rates, minimize time spent foraging during the non-breeding season (Stalmaster and Gessaman 1984), have low wing-loading, and migrate by energy efficient thermal soaring and gliding (Kerlinger 1989; Hedenström 1993, 1997). Eagles can also withstand days of fasting after

gorging on salmon. This favorable combination of physiological and morphological attributes reduces the importance of gaining mass at stopovers, which may give eagles flexibility when deciding to resume migration.

Juvenile Bald Eagles stayed at Hauser Reservoir significantly longer following capture than older eagles. When similar age effects existed in other species, older birds were in better physiological condition (Serie and Sharp 1989, Ellegren 1991, Yong et al. 1998). However, eagles of different age classes were in similar condition, which further supported the pattern that body condition has little effect on stopover behavior. Hedenström (1997) reported that juvenile eagles migrated slower than older eagles from Europe to Africa, a pattern that might be caused by longer stopovers.

In contrast to other studies on fall migrants (e.g., Ellegren 1991, Yong et al. 1998), consumption rates, an indicator of mass gain, did not explain age-specific stopover behavior of Bald Eagles. Although juvenile and 1.5 year old eagles had similar daily consumption rates, these two age groups differed in post capture residence times. Interestingly, 1.5 year old eagles exhibited stopover behavior similar to older eagles. Several factors may have accounted for this pattern: experience gained during previous migrations (see Hedenström 1997), age-specific differences in muscle development, or age-specific expression of genetically-controlled impulses. However, annual mortality of juveniles and 1.5-year old eagles was similar (Harmata et al. 1999), and cannot account for such a striking age effect in stopover behavior.

Some species establish temporary feeding territories and/or exhibit interference competition at migratory stopovers (Rappole and Warner 1976; Lindström et al. 1990; Moore

and Yong 1991; Carpenter et al. 1993a, b). Under these circumstances, poor competitors, usually juveniles, have low consumption rates, which causes them either to leave densely populated stopovers quickly in search of unoccupied areas or to have longer stopovers as they attempt to replace fat reserves. Dominance in Bald Eagles is based not on age but size (Garcelon 1990), and females are larger than males (Bortolotti 1984, Garcelon et al. 1985). The high incidence of food piracy [$> 45\%$ of foraging attempts (Restani 1997)] among foraging eagles at Hauser Reservoir suggests that stopover behavior should differ between subordinates (males) and dominants (females), yet residence time following capture was not sex-specific. The superabundant prey base may compensate for food lost to pirating conspecifics and thus support even poor competitors (see also Stalmaster and Gessaman 1984).

I found no correlation between date of capture and post capture residence time. This result was unexpected because post capture residence time of Bald Eagles at an autumn concentration in nearby (270 km) Glacier National Park, Montana was negatively correlated with capture date (McClelland et al. 1994). Two factors might have accounted for the difference between our studies. First, more eagles were radio-tagged at Hauser Reservoir before eagle numbers peaked compared to those tagged at Glacier National Park ($\chi^2 = 10.39$, $df = 1$, $P = 0.001$; McClelland et al. 1994: fig. 10). Whether eagles captured late in the season at Glacier had just arrived at the concentration or had been there for several days and were preparing to depart could not be determined. Second, 7 of 9 December departures from Glacier were of eagles captured in December, whereas I did not capture eagles past November. These differences in sampling may have created a false impression of seasonal effects.

Body condition of Bald Eagles did not correlate with post capture residence time, a result consistent with the hypothesis that eco-physiology of this large species (e.g., low mass-specific metabolic rate, migration using soaring flight) influences stopover behavior. Body condition and consumption rates did not explain the significant difference in stopover behavior between juveniles and older eagles.

Resource depression was not a reason for eagles to leave Hauser Reservoir because consumption rates remained constant. Most eagles (94%) continued their migration in November, weeks before salmon abundance dropped in December. Eagles left the stopover continuously during autumn, rather than in large groups on certain days.

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